








Research Article

Slipped through the narrow door: Effects of climate change on the distribution and conservation of a vulnerable tiger gecko, *Goniurosaurus luyi*, from China and Vietnam

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Abstract

Under human impacts, the global effects of climate change are exacerbating the biodiversity crisis with an anticipated high level of extinction risk for many species. As a range-restricted tropical specialist existing in small and fragmented populations, the likelihood of survival under future climate change is significantly reduced for *Goniurosaurus* species due to the loss of genetic diversity caused by population declines and habitat destruction. Predictions indicated that three Vietnamese tiger gecko species (*G. catbaensis*, *G. lichtenfelderi* and *G. huuliensis*) will be potentially impacted by climate change. It is projected that similar scenarios of climate change may also affect a highly specialized species, *G. luyi*, restricted to karst habitats in mainland southern China and northern Vietnam. In this study, we develop a species distribution model using MaxEnt, trained on climatic data to project the current potential distribution of *G. luyi*. To assess future impacts of climate change, we used climate change scenarios of three Shared Socioeconomic Pathways (i.e. ssp245, ssp370, ssp585) over 20-year periods (i.e. 2050s, 2070s and 2090s). Our models projected the potential distribution of *G. luyi* mainly covering the sites of occurrence and their surroundings in the border between China and Vietnam, among which 3,175 km² are karst habitats containing highly climatic suitability. All scenarios of climate change projected a significantly smaller area of high suitability compared to the current prediction and even no highly suitable habitat was documented in pathways of ssp370 by 2070s and 2090s, and ssp585 by 2090s. Given the potential impacts of climate change in the future, we highlight the border area between China (e.g. southern Guangxi Province) and Vietnam (e.g. northern Cao Bang and Lang Son provinces) as priority region for habitat protection.

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Key words: Border area, conservation, future scenarios, human impacts, maximum entropy, potential distribution

Introduction

Under human impacts, the global effects of climate change, including elevated CO₂ levels, rising temperatures, altered precipitation patterns, rising sea levels, and the exacerbated increase in natural disasters, contribute to the biodiversity crisis that is forecasted in the future, resulting in declines across genetic, species, and ecosystem levels. As ectotherms, reptiles are more vulnerable to climate change because they rely on external temperatures to regulate their body functions, making them particularly sensitive to rising temperatures and environmental changes that disrupt their thermoregulation, reproduction, and habitat availability (Huey et al. 2009; Sinervo et al. 2010; Sunday et al. 2011; Gunderson and Leal 2012; Halstead and Schwanz 2015; Seebacher et al. 2015; Abram et al. 2017; Diele-Viegas et al. 2020; Cox et al. 2022; Díaz et al. 2022; Hayden and Blom 2024). Accordingly, more than one-third of global lizard species are projected to be at risk of extinction by the 2080s due to their limited capacity to adapt to rising temperatures or shift their ranges in response to climate change, with range-restricted tropical species being especially vulnerable (Deutsch et al. 2008; Huey et al. 2009; Sinervo et al. 2010; Laspiur et al. 2021).

Due to the high level of local endemism and small population sizes, all tiger gecko species of the genus *Goniurosaurus* found in Japan (Ryukyu Archipelago), southern China, and northern Vietnam, are particularly vulnerable to human impacts, which may amplify the unprecedented effects of climate change (Grismer et al. 1999; Ngo et al. 2016; Le et al. 2017; Ngo et al. 2019a, 2019b, 2021a, 2022a, 2023). A recent study by Ngo et al. (2023) identified that most species of Chinese and Vietnamese groups follow an evolutionary pattern of niche conservatism, adapting to convergent niche gradients and maintaining their ancestral niche preferences. This evolutionary pattern restricts their ability to adapt to rapid climate shifts, making these species groups more susceptible to climate change. Exhibiting a contrary pattern of niche divergence, two Vietnamese species *G. catbaensis* and *G. lichtenfelderi* were forecasted to be less susceptible to climate change (Ngo et al. 2023). However, species distribution models (SDMs) using future scenarios of climate change projected that the current potential distribution of the three tiger gecko species *G. catbaensis*, *G. lichtenfelderi* and *G. huuliensis* tends to shrink significantly and shift towards higher latitudes (Le et al. 2017; Ngo et al. 2021a, 2022a). Their survival likelihood under future climate change has even been reduced decisively by the loss of genetic diversity that likely occurs in all *Goniurosaurus* species due to population declines and habitat loss (Le et al. 2017; Ngo et al. 2019b, 2022a, 2022b, 2023).

The Lui tiger gecko, *Goniurosaurus luii*, was first discovered in southern China and afterwards found in some provinces of Cao Bang and Lang Son, northern Vietnam (Fig. 2A) (Grismer et al. 1999; Vu et al. 2006). Ngo et al. (2022b) provided novel data on microhabitat use of *G. luii* and identified the species as a karst forest specialist. However, limestone forest mountains, the habitats of *G. luii*, have been strongly fragmented due to timber logging activities, quarrying to extract materials for cement production, and to expand road construction

and infrastructure (Ngo et al. 2022b). Similar to some other gecko species in Vietnam, the unsustainable exploitation of *G. luei* by trading the species in large quantities both domestically and internationally has led to local extirpations (Grismer et al. 1999; Yang and Chan 2015; Lindenmayer and Scheele 2017; Ngo et al. 2019b). Consequently, *G. luei* has been included in the IUCN Red List for Threatened Species as Vulnerable (VU), in CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix II (CITES 2025), and the Vietnam Government's Decree No. 84/2021/ND-CP (Group IIB).

In this study, the maximum entropy algorithm (MaxEnt) was used to predict the potential distribution of *G. luei* by combining distribution records and gridded data sets of climatic conditions of temperature and precipitation. We further evaluate its alterations under different future scenarios. Like other *Goniurosaurus* species, *G. luei* is characterized by a high level of habitat specialization, low dispersal ability, low population sizes and/or low levels of genetic diversity (Ngo et al. 2016, 2022b, 2023). Aforementioned traits are likely to make the species more vulnerable to climate change. We hypothesize that suitable habitats of *G. luei* will contract significantly due to climate change and its effects will become worse under severe human impacts. Based on the simulated outcomes, we identify potential core habitats safeguarding wild populations of *G. luei*, with reference to improving the efficacy of conservation measures.

Methods

The study site

The study area for all predictions was defined within latitudes of 20–24°N and longitudes of 104–109°E (Fig. 2) as the background (218,176 km²). This area covers the known distribution locations of the five Vietnamese *Goniurosaurus* species (i.e. *G. araneus*, *G. catbaensis*, *G. huiliensis*, *G. lichtenfelderi* and *G. luei*), occurring in northern Vietnam and southern China (Grismer et al. 1999; Vu et al. 2006; Orlov et al. 2008; Ziegler et al. 2008; Nguyen et al. 2009; Ngo et al. 2021a, 2023). Accordingly, *G. luei* is known from the karst forest mountains from southern China (e.g. Guangxi Province) and northern Vietnam (e.g. Cao Bang and Lang Son provinces). Grismer et al. (1999) documented a population of *G. luei* on the Hainan Island (China), but taxonomic re-assessments confirmed that all *Goniurosaurus* populations on this island belong to the monophyletic *G. lichtenfelderi* group (Grismer et al. 1999; Zhu et al. 2020).

Data collection

To project the current potential distribution of species, we obtained 19 bioclimatic variables from Worldclim 2.1 (Fick and Hijmans 2017) at 30 arc seconds resolution. For future projections, we used a global circulation model (GCM) of Meteorological Research Institute Earth System Model (MRI-ESM2-0) of the sixth Coupled Model Intercomparison Project (CMIP6) (Eyring et al. 2016; Yukimoto et al. 2019), developed by the Meteorological Research Institute in Japan. This climate model is able to capture regional monsoon dynamics, to simulate ocean-atmosphere interactions, and to predict tropical cyclone behavior. Three climate change scenarios of the Shared Socioeconomic Pathways

(SSPs) were downloaded to assess the different level of climate change impacts over 20-year periods (i.e. 2050s: 2041–2060; 2070s: 2061–2080; 2090s: 2081–2100): ssp245 (“middle of the road”: temperatures are projected to rise by 2.7 °C by the end of the century), ssp370 (“regional rivalry”: to rise by around 3.2 °C to 4.1 °C) and ssp585 (“fossil-fuelled development”: to rise by around 4.7 °C to 5.1 °C) (O’Neill et al. 2016; Riahi et al. 2017).

We compiled a total of 24 occurrence records from the Global Biodiversity Information Facility (GBIF) using the “rgbif” package in R v 3.8.1, among which the two coordinates from Hainan Island, China were omitted due to the misidentification of *G. luyi* (Grismer et al. 1999, 2021; Chamberlain et al. 2024; GBIF 2024; R Core Team 2024). Coordinates of 97 records of *G. luyi* were added from literature, from interviews with local people and approved by direct observations during field surveys. We subsampled the total dataset of coordinates by deleting neighboring points and randomly selecting only one record in a radius of 1 km, and each record was fitted into a pixel with the same resolution of climate data, using the “dismo” package in R (Aiello-Lammens et al. 2015; Hijmans et al. 2022). Finally, 45 representative occurrence records of *G. luyi* were employed for further analyses (Fig. 2A).

To mitigate the influence of potential multicollinearity of predictors on the models, a pairwise Pearson correlation analysis of 19 climatic conditions was conducted, using the “usdm” package in R to identify and eliminate highly correlated environmental variables with coefficient values larger than |0.75| (Dormann et al. 2013; Naimi 2015). Our final dataset comprised six variables including Mean Diurnal Range (Bio2), Temperature Seasonality (Bio4), Max Temperature of Warmest Month (Bio5), Annual Precipitation (Bio12), Precipitation of Driest Month (Bio14) and Precipitation Seasonality (Bio15), which were selected for subsequent analyses.

Species distribution modeling

Occurrence data of *G. luyi* and six selected climate variables under current conditions were imported into the MaxEnt software v. 3.4.3 (Phillips et al. 2006), to predict the potential distribution under current and future scenarios.

In order to minimize model overfitting due to the low number of presence locations (Shcheglovitova and Anderson 2013; Muscarella et al. 2014), we used the ENMeval package version 2.0 (Kass et al. 2021) in R to determine the optimal model parameter configuration by varying the “feature” and “regularization multiplier” parameters for our models. First, we randomly sampled 10,000 background points across the entire study area using the “randomPoints” function of the dismo package (Hijmans et al. 2022). Next, we generated 4-fold spatial blocks to generate a default model. We then used this default model to test model hyperparameters with 13 feature combinations (L, Q, H, P, LQ, LP, QH, QP, HP, LQH, LQP, LQHP and LQHPT; where L = linear, Q = quadratic, H = hinge, P = product, T = threshold) and regularization values ranging from 0.5 to 5 with a 0.5 increment, using the “gridSearch” function of the SDMtune package in R. A total of 130 candidate models were evaluated using spatial block cross-validation and the area under the receiver operating characteristic curve (AUC) calculated by the training (AUC_{TRAIN}) and testing data (AUC_{TEST}). To select

a model with a low degree of overfitting and high predictive performance, we retained the best optimal parameter, based on the highest AUC_{TEST} and the lowest AUC_{DIFF} ($AUC_{TRAIN} - AUC_{TEST}$) (Warren and Seifert 2011). Based on these filtering criteria, the final SDM for *G. luei* was generated with the feature classes LQHPT and a regularization value of 0.5.

We ran 100 bootstrap replications by sampling with replacement from the presence (Phillips et al. 2006). Default values were applied for the maximum number of interactions (500), the maximum number of background points (10,000), and the prevalence of the species (0.5) (Phillips and Dudík 2008). Lastly, we selected the cloglog output format, in which values ranging from 0 to 1 indicate the probability of suitable environmental conditions for the species. In particular, values closer to 1 suggest a greater probability of species occurrence. The AUC score was used to evaluate the predictive performance, ranging from 0 to 1 (perfect performance). The contribution of each variable to the current climatic model was determined by measuring the permutation importance and contribution percentage (Phillips and Dudík 2008). The minimum training presence threshold was selected in MaxEnt to convert continuous predicted values to binary maps of suitable and unsuitable areas, ensuring the minimum likelihood of species presence with higher values of the threshold (Phillips et al. 2006; Peterson 2011). We further used the higher threshold of 10% training omission cloglog, focusing projections on the core suitable habitats (Phillips et al. 2006).

In this study, we identified the region of “Stability” (overlapped suitable habitats between current and future predictions), the region of “Loss” (current suitable habitats uncovered by the future prediction) and the region of “Expansion” (future suitable habitats uncovered by the current prediction). To calculate their area and percentage with the “raster” package in R (Hijmans 2023), each raster cell with a resolution of 30 arc-seconds in EPSG4326, was classified with “Stability”, “Loss” or “Expansion” within the study site. Subsequently, the number of identified raster cells by the area was multiplied to calculate the total area in square units (km²) (Hijmans 2023).

To assess the predictive capabilities of the current model, a multivariate environmental similarity surface (MESS) analysis that was used to quantify potential extrapolation errors, was developed in recent versions of MaxEnt (Elith et al. 2010). This analysis compares the environmental similarity of any given grid cell within the projection range of the models to the environmental training range of the models. It is used to identify extrapolation in areas characterized by novel environmental conditions, which are beyond the training range of the models, indicated by negative values (Fitzpatrick and Hargrove 2009; Elith et al. 2010). In this study, novelty and similarity were classified into levels of extrapolation (negative values) and interpolation (positive values), respectively. We also performed MESS analyses to create maps for each future climate scenario and to evaluate the alteration of reference conditions under the current climate model.

Furthermore, values of these six climatic variables were extracted from the occurrence records of *G. luei* in the present and future scenarios to assess the novelty of conditions under climate change, using the “raster” package in R (Hijmans 2023). The current climatic values were compared to those of each future scenario by using t-tests, with a significant level of $P \leq 0.05$.

Core distribution areas

To enhance the efficacy of conservation projects for range-restricted species of *Goniurosaurus* with a limited dispersal capacity (Grismer et al. 2021; Ngo et al. 2022b, 2023), a spatial dissolved buffer with a radius of 80 km around occurrence points with an area of 89,181 km² was generated using the R packages “dismo” and “raster”. This area is expected to encompass all potential distribution for *G. luei*. We identified the core habitats within the boundary of buffer layer containing highly suitable areas in terms of climate, which have values above 10% training omission cloglog threshold (high occurrence probability). This is a stricter criterion for converting to a binary map of higher suitable habitats (Radosavljevic and Anderson 2014) that was layered with the extracted karst layer from the World Karst Aquifer Map (Goldscheider et al. 2020), due to *G. luei* is identified as a karst-adapted specialist (Grismer et al. 1999, 2021; Ngo et al. 2022b). Finally, maps were generated using Quantum GIS software (QGIS Version 3.12.0, 2020), showing the study site, buffer, suitable habitats within the study site, buffer layer, and layered with the karst site.

Results

The optimized model (LQHPT-feature and 0.5-regularization) presented a high average training AUC of 0.988. The most important climate variable is the Temperature Seasonality (Bio4), followed by Precipitation of Driest Month (Bio14), Precipitation Seasonality (Bio15) and Annual Precipitation (Bio12), all of which accounted for 91% of model contribution and 88.2% permutation importance (Fig. 1, Suppl. material 1: fig. S1, Suppl. material 2: table S1). According to the response curves of the climatic variables, MaxEnt predicted the potential distribution of *G. luei* in areas, where the temperature seasonality (standard deviation \times 100) ranged from 451.5 to 625.7, the precipitation of driest month ranged from 7 to 34 mm, precipitation seasonality (Coefficient of Variation) ranged from 73.3 to 92.1, and annual precipitation ranged from 1,042 to 2,081 mm/year (Fig. 1).

MaxEnt predicted the highly suitable habitats of *G. luei* almost covering the border regions of Guangxi Province, China, and Cao Bang and Lang Son provinces, Vietnam under current conditions (Fig. 2D). Habitats of low climatic suitability were projected in the south of Lang Son Province and other Vietnamese provinces of Bac Kan, Ha Giang, Quang Ninh, Thai Nguyen, Tuyen Quang, Vinh Phuc, Yen Bai, and some Chinese districts of Guangxi and Yunnan provinces (Fig. 2B, C).

We calculated the total area of suitable habitats representing approximately 24,250 km², of which more than 90% (21,987 km²) were identified within the buffer site, and even a total of highly suitable habitat of *G. luei* located in the buffer site (Fig. 2D; Table 1). Being a karst-adapted species, *G. luei* was predicted to inhabit the smaller area of 15,407 km² within the karst buffer, containing highly suitable habitats of 3,175 km² (~20.6%; Table 1). With the current MESS projection, interpolated habitats covered the entire buffer site (Fig. 2C). Given future predictions, in general, the climatically suitable area fluctuated among periods of 2050s, 2070s and 2090s for each pathway (e.g. ssp245, ssp370 and

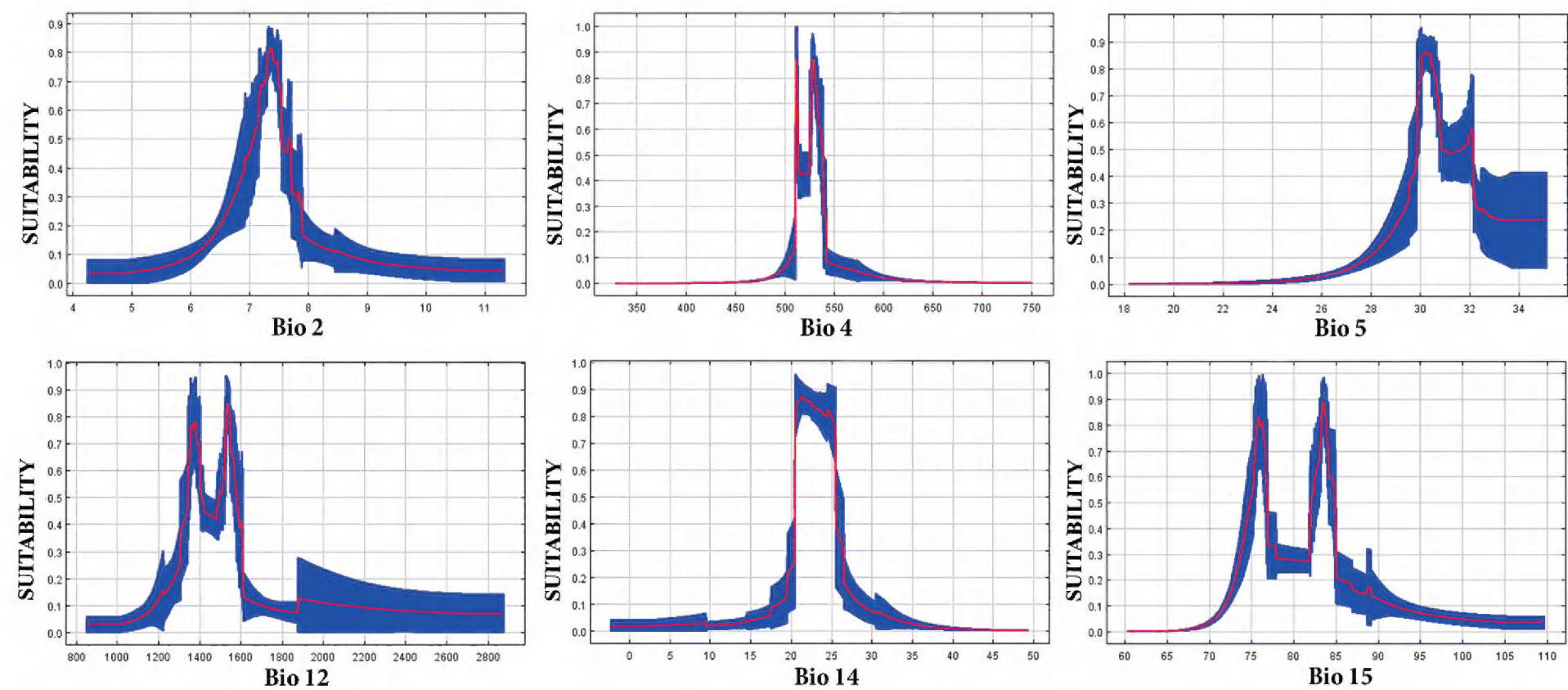


Figure 1. Response curves of six selected climatic variables to the probability of suitability.

Table 1. Projected areas of suitable habitats for *Goniurosaurus luyi*.

	Areas of suitable habitats (Minimum Threshold) (km ²)				Areas of highly suitable habitats (10% Threshold) (km ²)			
	Total	Buffer	Karst_Total	Karst_buffer	Total	Buffer	Karst_Total	Karst_buffer
Current	24,250	21,987	16,616	15,407	3,405	3,405	3,175	3,175
ssp245_2050s	29,168	23,511	20,408	16,848	1,597	1,597	1,346	1,346
ssp245_2070s	41,415	30,878	28,035	20,966	1,060	1,060	972	972
ssp245_2090s	54,598	32,260	36,610	21,737	105	105	32	32
ssp370_2050s	47,295	33,192	30,249	21,405	52	52	2	2
ssp370_2070s	52,922	35,654	35,379	24,745	96	96	13	13
ssp370_2090s	31,004	12,521	22,031	9,963	0	0	0	0
ssp585_2050s	37,582	30,537	26,407	21,569	1,553	1,553	1,430	1,430
ssp585_2070s	37,221	28,058	25,736	18,507	78	78	38	38
ssp585_2090s	44,331	21,217	31,949	13,727	0	0	0	0

ssp585) (Fig. 4, Suppl. material 1: fig. S3). The MESS projections of future scenarios documented a replacement from some interpolated habitats at present to novelty (extrapolated) habitats in the future (Fig. 2). Current climatic conditions of *G. luyi*'s occurrences were significantly different to novel conditions of future scenarios as well (t-tests, P-values < 0.01; Fig. 3; Suppl. material 2: table S2). Using the threshold value of above 10% training presence cloglog to identify the higher suitability, all scenarios of climate change projected a significantly smaller area of suitable habitats compared to the current prediction (Figs 5, 6; Suppl. material 2: table S1). It is noteworthy that novel climatic conditions were recorded in the entire study area in all scenarios of three pathways in the period of 2090s and no highly suitable habitat for *G. luyi* was documented (0 km²) in the pathways of ssp370 and ssp585 at that time and in the scenarios of ssp370 in 2070s (Figs 5, 6; Table 1). Suitable habitats – “Stability” projected between the present and future periods overlapped with less than 35%, whereas both uncovered areas of “Loss” and “Expansion” between them are even more than 90% (Fig. 7; Suppl. material 2: table S3).

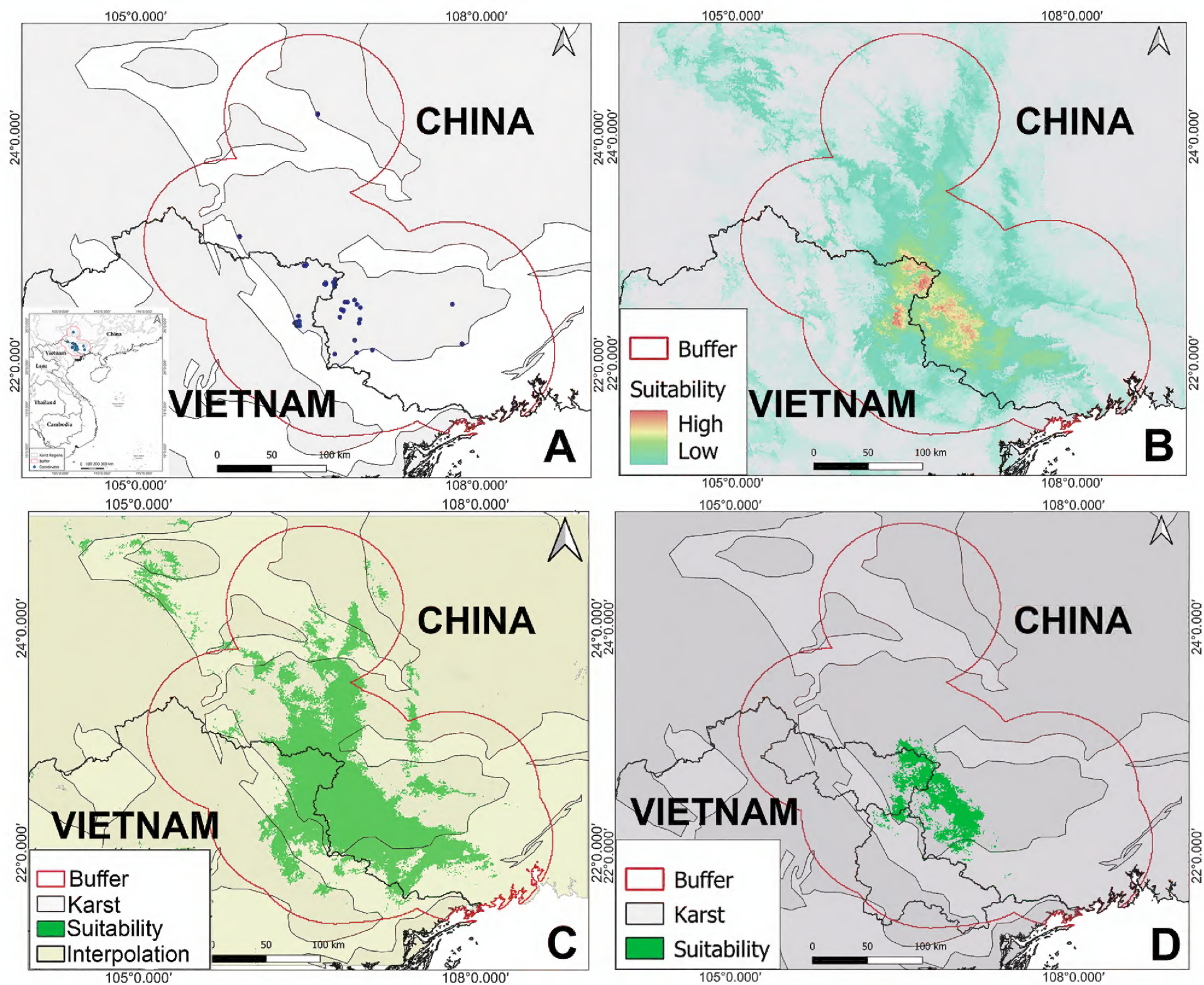


Figure 2. The prediction of potential distribution of *Goniurosaurus luii*. **A.** Occurrences on the karst background; **B.** The potential distribution in the present; **C.** Suitable habitats with the minimum training presence threshold (Yellow indicating the interpolated prediction of multivariate environmental similarity surface (MESS) analyses); **D.** Core refugia containing highly suitable habitats with 10% training presence cloglog threshold, within the karst area.

Discussion

Selected climates

Owing to the ectothermic characteristics, climatic variables may influence the spatial distribution of *G. luii* (Lopez-Alcaide and Macip-Rios 2011; Vicente et al. 2019; Ngo et al. 2022b). The species is known in the region of tropical monsoon climate with a significant seasonal difference in temperature in southern China and northern Vietnam (Nguyen and Vu 2015), accounting for why the climatic condition of Temperature Seasonality (Bio4) is the most important predictive variable (nearly 50% contribution) in the current model. The model predicted moderate temperature variability throughout the year (ranged from 451.5 to 625.7) that is suited to preferred mid-altitude habitats of *G. luii* (Ngo et al. 2022b). The projected potential distribution was characterized by the relatively low precipitation in the driest month (from 7 to 34 mm; Fig. 1) occurring in the winter (Nguyen and Vu 2015). Thus, the precipitation seasonality ranging from 73.3 to 92.1 indicates a high variability in rainfall throughout the year,

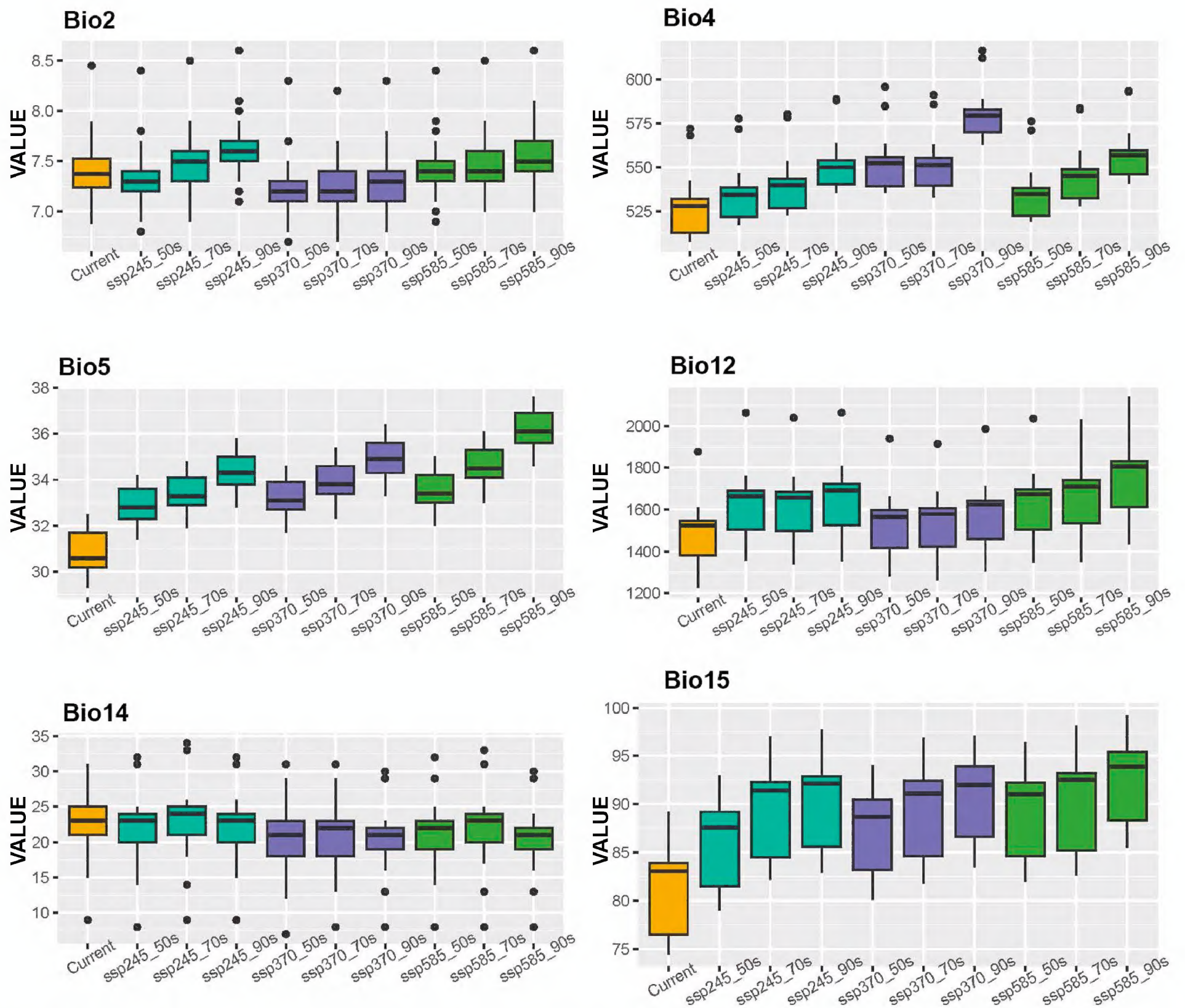


Figure 3. Extracted values of six selected climatic conditions from the *Goniurosaurus luei*'s occurrences in the present and the future under different scenarios of climate change.

with a significant difference between the wettest and driest months, and annual precipitation ranged from 1,042 to 2,081 mm/year (Fig. 1), all of which characterize the typical tropical monsoon climate covering the habitats of *G. luei* (Nguyen and Vu 2015; Fick and Hijmans 2017).

Potential distribution

As expected, the model suggested under current conditions that the highly suitable habitats for *G. luei* are primarily located in the sites of occurrence (Fig. 2D). New populations may potentially be found in southern Lang Son and Thai Nguyen provinces, given the known distribution of *G. huuliensis*, as well as Quang Ninh Province, Vietnam, and Chongzuo and Fangchenggang districts, China, given as a part of *G. lichtenfelderi*'s habitat range (Orlov et al. 2008; Zhu et al. 2020; Ngo et al. 2021a, 2022a, 2022b). Additionally, areas in Yunnan Province, China and other provinces of Vietnam, viz. Bac Kan, Tuyen Quang, Yen Bai, Ha Giang and Vinh Phuc, may harbor undiscovered populations of *G. luei* (Fig. 2). However, previously extensive surveys confirmed that in these patches of the

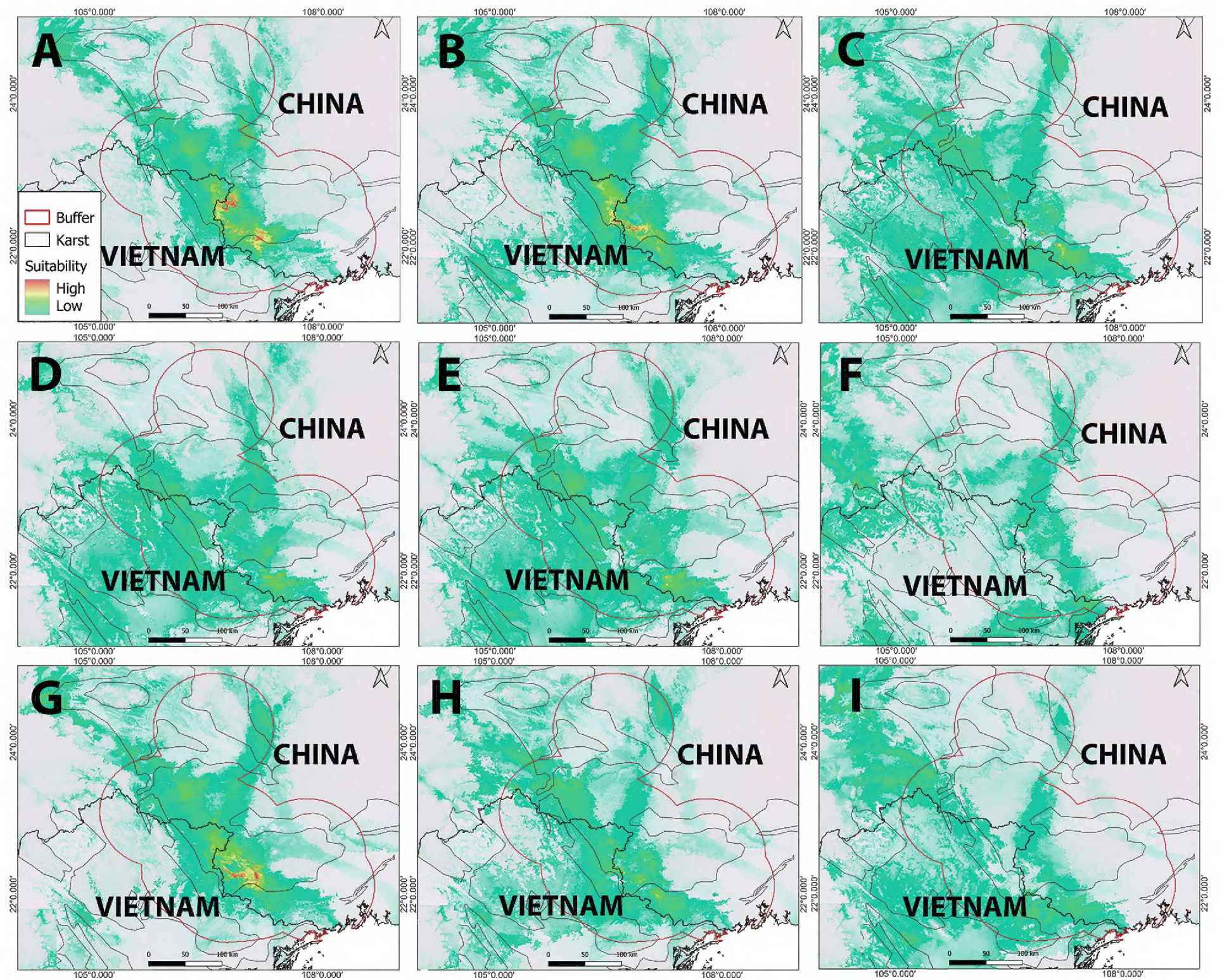


Figure 4. Projected potential distribution with the minimum training presence threshold for *Goniurosaurus luyi* under different future climate scenarios. **A.** ssp245 by the 2050s; **B.** ssp245 by the 2070s; **C.** ssp245 by the 2090s; **D.** ssp370 by the 2050s; **E.** ssp370 by the 2070s; **F.** ssp370 by the 2090s; **G.** ssp585 by the 2050s; **H.** ssp585 by the 2070s; **I.** ssp585 by the 2090s.

potential distribution, *G. luyi* does not occur sympatrically with other tiger geckos and in projected low suitability habitats, except for some potential regions in Chongzuo District, Guangxi Province, China (Ngo et al. 2021a, 2021b, 2022b).

Climate change

Since locally distributed specialists adapt to unique niches and having small population sizes, all tiger geckos of *Goniurosaurus* are highly vulnerable to climate change (Grismer et al. 2021; Ngo et al. 2023). Our future models showed the opposite result that suitable habitats forecasted by using scenarios of climate change document a larger area than that projected by the current model. However, most future scenarios will expand the suitable habitats (Expansion) of more than 50%, and the overlapped layers between current and future suitable habitats only cover areas of stability less than 35% (Suppl. material 2: table S3). We further acknowledge that some current interpolated habitats and extracted climatic conditions of occurrences, especially Temperature Seasonality (Bio4) and Annual Precipitation (Bio12), are extrapolated to future novel

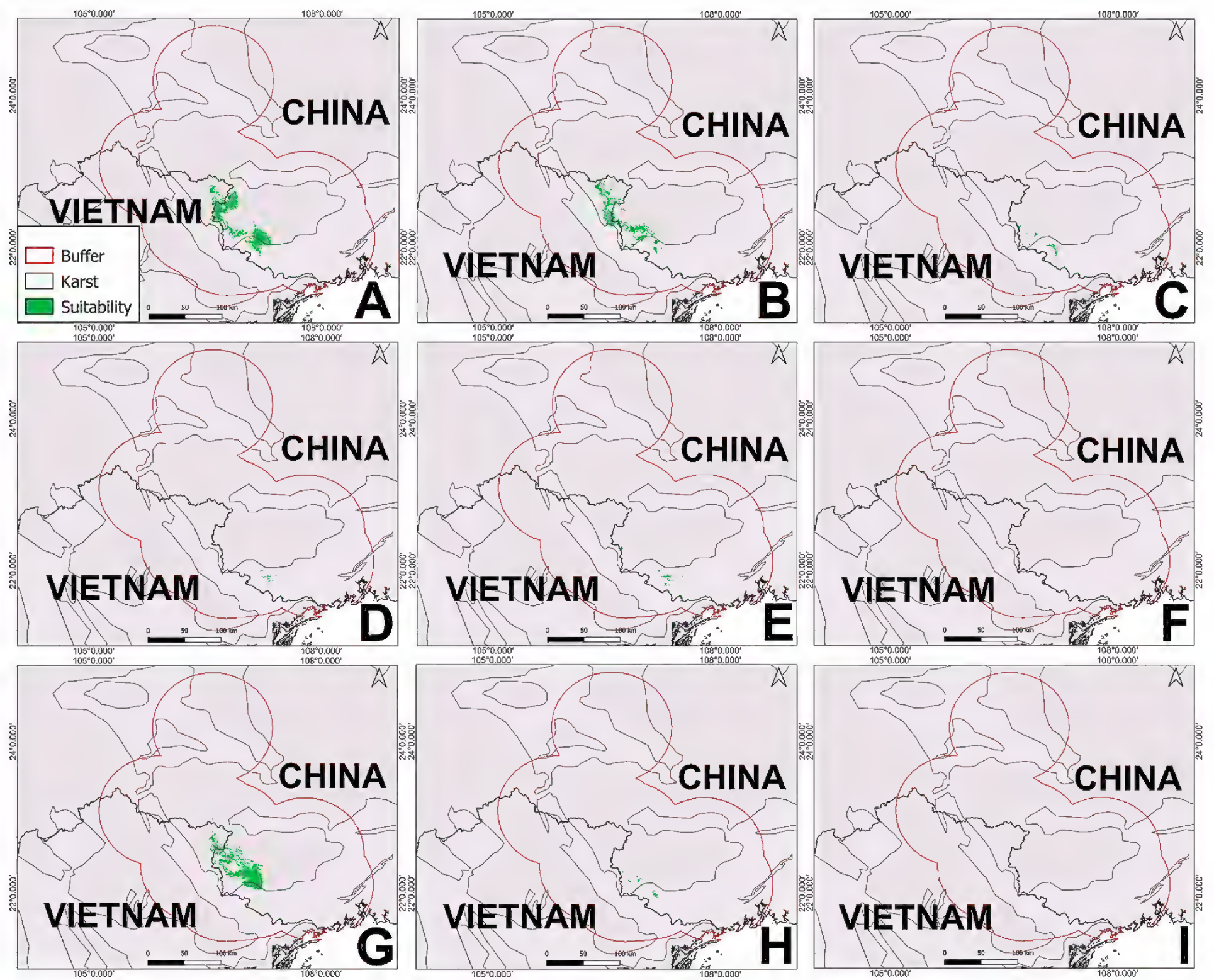


Figure 5. Highly suitable habitats with 10% training presence cloglog threshold, for *Goniurosaurus luei* under different future climate scenarios. **A.** ssp245 by the 2050s; **B.** ssp245 by the 2070s; **C.** ssp245 by the 2090s; **D.** ssp370 by the 2050s; **E.** ssp370 by the 2070s; **F.** ssp370 by the 2090s; **G.** ssp585 by the 2050s; **H.** ssp585 by the 2070s; **I.** ssp585 by the 2090s.

conditions (Fig. 3, Suppl. material 1: figs S2, S3). Given highly suitable habitats, our model results agreed well with previous predictions in other tiger geckos of *G. catbaensis*, *G. huiliensis* and *G. lichtenfelderi* that their current potential distribution somewhat tends to narrow in the future (Le et al. 2017; Ngo et al. 2021a, 2022b). It is noteworthy that the potential distribution of *G. luei* will vanish in the entire study area and will be completely enveloped under novel climatic conditions in the future scenarios of ssp370 and ssp585 by the 2090s, and be mostly replaced following other scenarios of ssp370 (Figs 5–7).

Adaptability and conservation

Species’ success in adapting to climate change will rely on the velocity of climatic alterations and their capacity for dispersal. The high rate and intensity of climate change today, including temperature increases, extreme weather events, and sea level rise, are historically unprecedented (IPCC 2021). The biodiversity is globally shrinking rapidly with estimated current extinction rates of species that are 100 to 1,000 times higher than natural extinction rates (Pereira

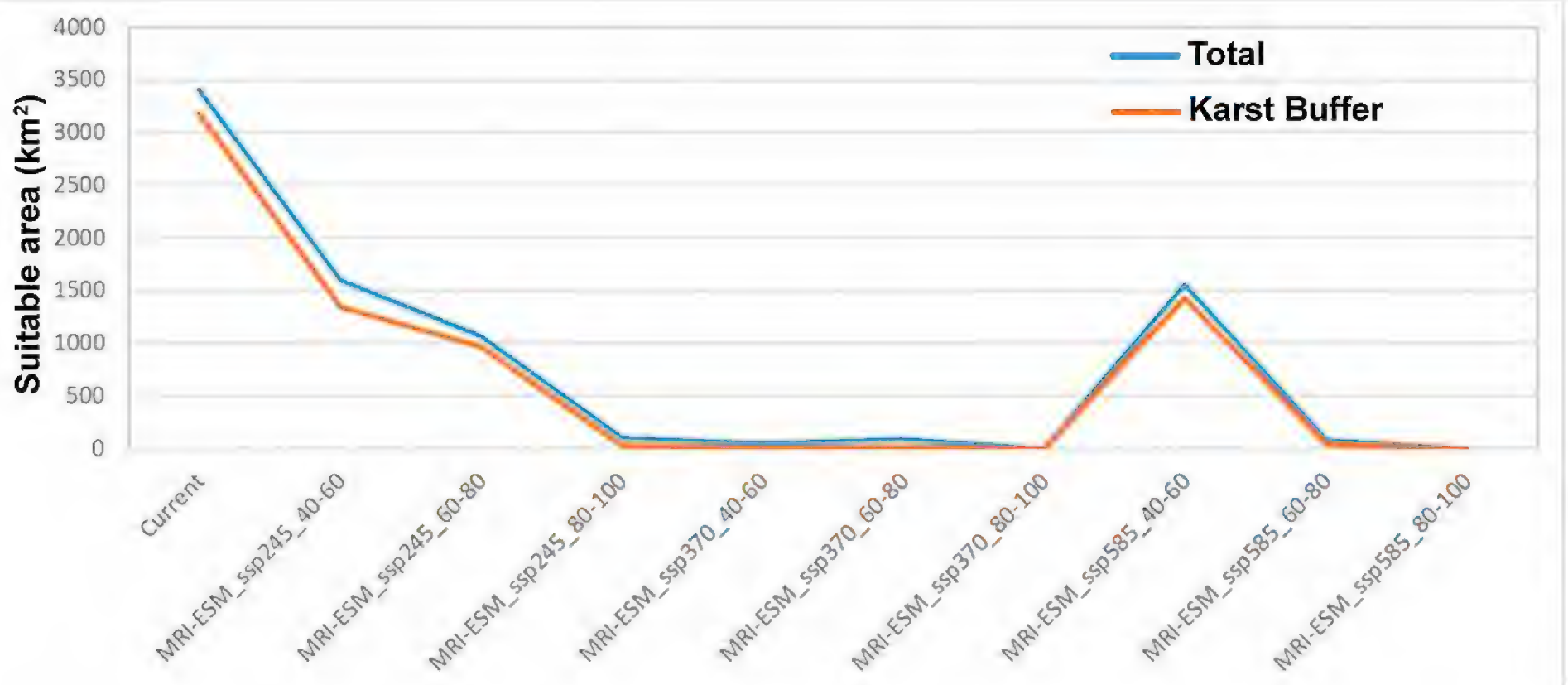


Figure 6. Projected areas of highly suitable habitats with 10% training presence cloglog threshold, for *Goniurosaurus luyi* under different climate conditions of current and future scenarios (blue line: areas within the study site; orange line: areas within the karst and buffer sites).

et al. 2010; Ceballos et al. 2015; Urban 2015). Indeed, the potential distribution of *G. luyi* was projected no longer to exist in some severe scenarios of climate change. Like some invasive species, *G. luyi* may itself undergo rapid niche shifts to novel environments of climate change through evolving environmental tolerances (fundamental niche shifts) (Broennimann et al. 2007; Alexander and Edwards 2010; Guisan et al. 2014; Li et al. 2014). However, given the potential for niche evolution, *G. luyi* was suggested to show a high rate of niche conservatism by retaining ancestral niches over time and presenting a low level of physiological tolerances to niche alterations (Wiens and Graham 2005; Hadly et al. 2009; Wiens et al. 2010; Peterson 2011; Ngo et al. 2023). Such species, including *G. luyi* may be more susceptible to climate change due to constraints in genetic variation, following the evolutionary pattern of niche conservatism limiting the likelihood of adaptation to changing conditions (Ngo et al. 2023). Meanwhile, the severe exploitation of *G. luyi* for the pet trade causes decreasing population size and genetic diversity, which hamper its natural adaptation, and even led to local extirpation in some populations from China (Grismer et al. 1999; Ngo et al. 2019b). On the other hand, the ability of susceptible species to persist, in the face of rapid climate change, will depend on their access to refugia that mitigate extreme conditions (Scheffers et al. 2014). Accordingly, a species can undertake range shifts towards optimal environments to avoid the extinction pressure of climate change (Sinervo et al. 2010). However, range-restricted tiger geckos are unable to migrate larger distances to climatic refugia due to either habitat specialization or unsettled forest corridors, even the refugia may not endure in the future (Ngo et al. 2021a, 2022b). Ngo et al. (2022b) identified *G. luyi* as an exclusive habitat specialist of karst formations covered by dense evergreen broad leaves forests. High levels of species diversity (e.g. in the genera *Cyrtodactylus* and *Cnemaspis*) are also documented in karst ecosystems, probably due to their disjunctive distribution and the multitude of ecological niches offered by complex topography and variable micro-climatic conditions (Clements et al. 2006; Wood et al. 2017; Grismer et al. 2021). Under

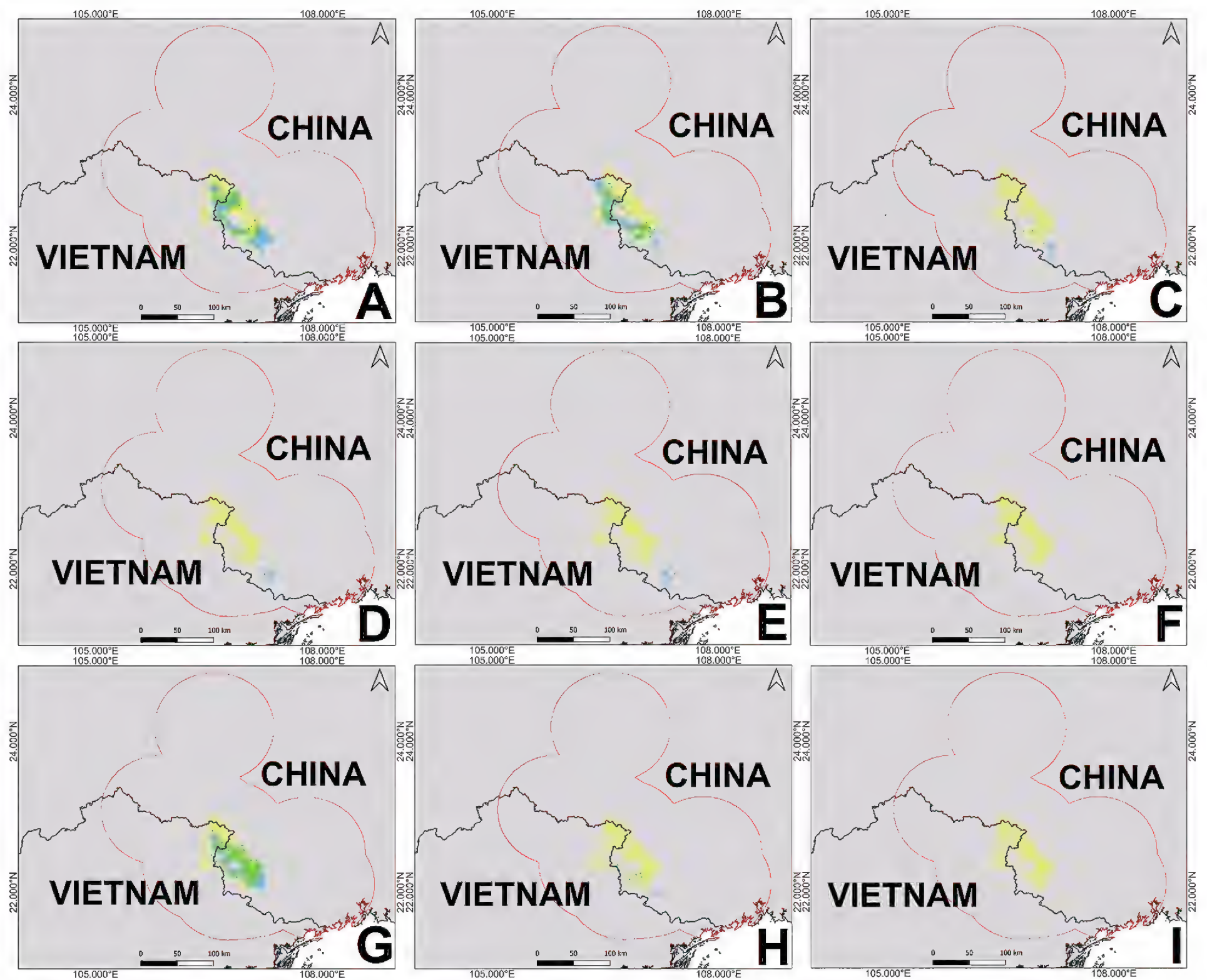


Figure 7. The range shift of highly suitable habitats with 10% training presence cloglog threshold, for *Goniurosaurus luii* under under different future climate scenarios. **A.** ssp245 by the 2050s; **B.** ssp245 by the 2070s; **C.** ssp245 by the 2090s; **D.** ssp370 by the 2050s; **E.** ssp370 by the 2070s; **F.** ssp370 by the 2090s; **G.** ssp585 by the 2050s; **H.** ssp585 by the 2070s; **I.** ssp585 by the 2090s. (Green color: Stability; Blue color: Expansion; and Yellow color: Loss).

climate change, the complex karst habitats likely construct unique micro-refugia containing favorable micro-climate conditions which could buffer the species diversity against suboptimal climates (Clements et al. 2006; Sterling et al. 2006). However, this last survival chance of *G. luii* and other karstic geckos is currently getting narrower due to the intensive loss of micro-refugia as a result of deforestation and quarrying in karst formations (Clements et al. 2006; Queiroz et al. 2013; CEPF 2020; Ngo et al. 2022b). Thus, based on the forecasted map of Fig. 2D, we highlight the green patches of karst habitats in the border area between China and Vietnam (Fig. 2D) as the most important core-refugia of *G. luii* for priority conservation of karst-forest protection.

Conclusions

Climate change is assumed to have significantly impact on *G. luii*, a highly specialized species restricted to karst habitats in mainland southern China and northern Vietnam. In this study, we developed a species distribution model

using MaxEnt, trained on climatic data, to project the current potential distribution of *G. luei*. To assess future climate change impacts, we applied three Shared Socioeconomic Pathways (ssp245, ssp370, and ssp585) over 20-year intervals (2050s, 2070s, and 2090s).

Our models indicated that the potential distribution of *G. luei* is distributed mainly in the China-Vietnam border region, with 3,175 km² of karst habitat classified as highly suitable. However, future climate projections showed a significant reduction in the suitable habitat of climate. By the 2070s and 2090s, no highly suitable areas remain under the scenario of ssp370, and by 2090, the scenario of ssp585 predicts a complete loss of such habitat.

Given these findings, we emphasize the urgent need for conservation efforts in the border regions of China (southern Guangxi Province) and Vietnam (northern Cao Bang and Lang Son provinces). Protecting the natural habitats of limestone karsts is crucial for mitigating climate change impacts and ensuring the long-term survival of *G. luei*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Huong Nguyen Thi Thu: Writing - Review and Editing, Visualization, Supervision. Linh Thuy Thi Ha: Methodology, Software, Validation, Formal analysis, Writing - Original draft. Truong Quang Nguyen: Conceptualization, Writing - Original draft, Writing - Review and Editing. Larry Lee Grismer: Writing - Original draft, Writing - Review and Editing. Dennis Rödder: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - Original draft, Writing - Review and Editing, Visualization, Supervision. Thomas Ziegler: Writing - Original draft, Writing - Review and Editing, Visualization, Supervision.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Additional images

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Data type: docx

Explanation note: **fig. S1.** Contribution percentage and permutation importance of selected climates. **fig. S2.** Suitable habitats with the minimum training presence threshold, for *Goniurosaurus luyi* under different future climate scenarios. A ssp245 by the 2050s; B ssp245 by the 2070s; C ssp245 by the 2090s; D ssp370 by the 2050s; E ssp370 by the 2070s; F ssp370 by the 2090s; G ssp585 by the 2050s; H ssp585 by the 2070s; I ssp585 by the 2090s (Yellow indicating the interpolated prediction of multivariate environmental similarity surface (MESS) analyses). **fig. S3.** The range shift of potential distribution with the minimum training presence threshold in study site for *Goniurosaurus luyi* under different future climate scenarios. A ssp245 by the 2050s; B ssp245 by the 2070s; C ssp245 by the 2090s; D ssp370 by the 2050s; E ssp370 by the 2070s; F ssp370 by the 2090s; G ssp585 by the 2050s; H ssp585 by the 2070s; I ssp585 by the 2090s (Green color: Stability; Blue color: Expansion; and Yellow color: Loss)

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Supplementary material 2

Additional tables

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Data type: docx

Explanation note: **table S1.** Contribution percentage (%) and permutation importance (%) of selected climates. **table S2.** Extracted climatic values of occurrences of *Goniurosaurus luyi* in the present and future scenarios of climate change (* indicating significant difference of the T-test). **table S3.** The percentage of range shift for *Goniurosaurus luyi* under different future climate scenarios.

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